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Feather River Salmon Spawning Escapement: a history and critique

Introduction

The number of salmon returning to spawn in a river each year is known as salmon spawning escapement. Accurate estimates of salmon spawning escapement are vital to evaluating stock status, guiding salmon management decisions, and providing for effective protection of endangered salmon stocks. Biased estimates can lead to flawed management plans and faulty assessment of water needs to protect or enhance fisheries (Hilborn and Walters 1992, Hinrichsen 2001). Increased attention and funding for salmon restoration activities throughout the Central Valley of California has placed an even higher premium on accurate spawning escapement data, which is often the only means of evaluating the necessity or success of restoration actions. Considering the weight and numerous applications of salmon spawning escapement data and the costs associated with errors, uncertainty in stock assessment clearly become very significant.

Salmon spawning escapement in most Central Valley rivers is currently assessed by applying mark-recapture techniques to salmon carcasses (Boydstun 1994). With this method, spawned-out salmon carcasses are recovered, tagged and placed back in the stream. Streams are surveyed weekly and the proportion of tagged carcasses recovered is used to estimate sampling efficiency. Total abundance is then projected by expanding the number of carcasses checked for tags by the sampling efficiency. This expansion is accomplished by applying one of several mark-recapture statistical models, with the Schaefer model being most popular.

On the Feather River, adult salmon escapement has been determined annually, using several different methods, since 1953. This sampling spans the period before the construction of Oroville Dam and start of operations for the Feather River Hatchery. This data set is therefore very useful in interpreting the effects of dam construction, and the success of mitigation actions (see Painter, Wixom and Taylor 1977). The purpose of this report is to: 1) summarize past salmon spawning escapement data from the Feather River, 2) present results from an expanded and improved year 2000 spawning escapement survey, 3) critically evaluate historic and recent spawning escapement data to assess potential errors and sources of bias, and 4) recommend actions which may improve the accuracy and reliability of spawning escapement data.

History of Feather River Salmon Spawning Escapement

Annual estimates of Feather River spawning escapement are available for both fall and spring-run chinook salmon. However, methods for estimating escapement have changed through time, and also differ between the two salmon races. Unfortunately, the precise methods used to generate past escapement estimates are often poorly documented. Several omnibus reports (Pacific Fishery Management Council 2001, Mills and Fisher 1994, for example) list annual escapement estimates for each river system but provide very little background information on how the estimate were calculated or other ancillary information. Department of Fish and Game (DFG) biologists have prepared regular annual reports for Feather River salmon escapement estimates since 1955. The information provided in these annual reports varies, but they almost always include some rationale for the ~~provided~~ escapement estimates. Details on sampling design and effort were generally absent however.

Estimates of fall-run escapement are split into two components: salmon entering the Feather River Hatchery and in-river spawners. The hatchery salmon component represents a count of individual ~~unique~~ salmon climbing the fish ladder and entering the hatchery from October through December each spawning year. In-river spawning has been estimated by several different techniques over the period of study. From 1953 through 1978, annual estimates of fall-run in-river spawners were determined by direct counts expanded relative to data from past years, or expanded by the percentage of the total population the direct count was thought to represent. Obviously, these techniques were highly subjective; year to year changes in spawning distribution (spatial or temporal) and the experience of the surveyors undoubtedly had a large impact on the accuracy of these estimates.

Due to the well-known limitations of these earlier methods, DFG began to employ mark-recapture techniques in 1979. The mark-recapture method was applied in every year after 1979, except for 1988, 1990 and 1998. In these years, an expanded index count was applied, much like those used prior to 1979. The precise sampling strategy (study design) and level of effort utilized in each year's mark-recapture survey is poorly detailed in annual reports. However, discussions with DFG biologists indicate that the surveys were conducted weekly, two days each week, utilizing one boat, staffed by two to four crew persons (Fred Meyer and Julie Brown, personal communication). The survey was divided into two distinct river reaches: Fish Barrier Dam to Thermalito Outlet and Thermalito Outlet to Gridley Bridge. Usually, one day was spent on each of these river sections, each section being about 8 river miles in length. In some years, surveys were extended several miles downstream of the Gridley Bridge. Overall, the typical survey area covered approximately 16 river miles. This is a vast area for one survey crew to search in two days. DWR habitat surveys indicate that this survey area includes at least 46 distinct riffle-pool sequences. Thus, a two-day survey of the area would require 2 riffle-pool sequences per hour be surveyed in order effectively cover the area in the allotted time. In light of the size of the Feather River and the abundance of its salmon runs, this seems an unrealistic goal. Indeed, conversations with DFG biologists and crew persons indicate that the river was neither sampled completely nor sub-sampled randomly. Instead spawning areas were haphazardly sub-sampled (at the discretion of the crew) in order to complete the survey in the time allowed. The implications of this sampling strategy for accuracy of escapement estimates will be discussed later.

Spring-run salmon spawning escapement on the Feather River has been estimated since 1954 using combinations of in-river estimates and hatchery counts. From 1954 through 1981, spring-run numbers in the Feather River were estimated by direct counts like those early estimates of fall-run in-river spawners. When the Feather River Hatchery began operations in 1967 spring-run were also counted based on the numbers of salmon entering hatchery during the month of September. Thus, estimates of spring-run numbers between 1967 and 1981 were a sum of in-river and hatchery estimates. After 1981, DFG ceased to estimate in-river spawning spring-run salmon because spatial and temporal overlap with fall-run spawners made it impossible to distinguish between the two races. Spring-run estimates after 1981 are based solely on salmon entering the hatchery during the month of September.

Estimates of in-river fall-run salmon demonstrate substantial variability during the period of record (Figure 1). An average of approximately 43,000 salmon have spawned in-river each year since 1954. These numbers have remained high even following the construction of the Oroville Dam and the Feather River Hatchery. An average of 8,300 salmon have entered the Feather River Hatchery each year since it opened (Figure 1). The number of hatchery salmon also appears to be increasing through this period. The high for the period of record occurred in the year 2000 when 123,400 salmon spawned in the Feather River while 21,200 salmon entered the Feather River Hatchery.

Following the completion of Oroville Dam and other upstream impoundments, spring-run estimates show a decline until the early eighties, after which abundance estimates increased substantially (Figure 2). The average spring-run estimate during the period of record was 2,115. The highest estimate occurred in 1988 with a total of 6,833 salmon entering the Feather River Hatchery in the month of September.

When interpreting data, it is always desirable to consider the data's accuracy and precision. Often with ecological data, such insights can be gained by comparing results from different sampling programs to see if similar trends are evident. Alternatively, replicated sampling programs can easily calculate confidence limits for abundance or density estimates. Annual escapement estimates however, are based on a single, un-replicated sample (albeit, a sample that is a composite of many samples collected over several months) and estimates are typically made using only one technique. Thus, opportunities for evaluating the quality of escapement data are rare. If accurate escapement estimates were easy to accomplish, the failure to assess potential error would not be a problem, but this is not the case. Whether escapement estimates are based on modified direct counts or mark-recapture techniques, they are subject to a considerable amount of error, and potentially severe bias in the final escapement estimate. Unfortunately, these potentially large errors are rarely taken into account by sampling programs or when spawning escapement data is applied for purposes of management or conservation.

Despite the difficulties of assessing the accuracy of Feather River escapement data, the long period of record, and operation of the Feather River Hatchery provide some opportunities for critical evaluation of fall-run spawning escapement estimates. The number of fall-run salmon entering the Feather River Hatchery each year provides an index useful in comparison with in-river estimates. Looking at the period of record (1967-2000), hatchery returns are positively correlated with in-river spawning, but explain only 15.9% of the observed variation (Figure 3). However, closer analysis reveals that even this relatively weak relationship is heavily influenced by one outlying data point, the year 2000 in-river estimate. With the year 2000 data point removed, the r^2 falls to 0.005 and the positive relationship is no longer significant, p=0.692 (Figure 4).

Analyzing the Low Flow Channel section (LFC) separately from below Thermalito Outlet section (THERM) yields somewhat different results. While separate escapement estimates by river section were not available for every year, the available data show a stronger positive relationship within the LFC (Figure 5). This result also is strongly influenced by the year 2000 data point. Removal of the outlying year 2000 point reduces the r^2 considerably (from 0.669 to 0.375), but the positive relationship remains significant, p=0.007 (Figure 6). THERM escapement estimates showed a very week positive relationship with hatchery returns, $r^2 = 0.07$, $p = 0.275$ (Figure 7). Interestingly, removing the year 2000 data point completely reverses this relationship (Figure 8).

The generally poor relationship between in-river abundance and the number of salmon returning to the Feather River hatchery has several potential explanations. First, hatchery returns may serve as a poor index of overall salmon abundance. The fact that a stronger, positive relationship exists within the LFC, than with total or THERM abundance estimates, suggests that the numbers of salmon entering the hatchery may be effected by local spawning distribution and not just overall run abundance. There may be years, for example, where total salmon spawning escapement is high, but salmon spawning is focussed downstream of Thermalito Outlet, and therefore relatively fewer salmon enter the Feather River Hatchery. While the relation between LFC and hatchery returns is significantly positive (i.e. non zero slope), it explains only 37.5% of the observed variation when the outlying year 2000 observation is removed. The significant positive relationship between these two variables surpasses only a minimum threshold of validity for Feather River escapement estimates. A positive relationship only demonstrates that the two abundance measures are proportional and says nothing about the precision or accuracy of the estimates. In fact, the low r^2 value suggests that there is substantial error associated with the current data set (poor precision). Two sets of data measuring ostensibly the same parameter (i.e. salmon spawner abundance) are expected to provide a much closer fit. Winter-run escapement estimates on the Sacramento River, for example, explained 95.9% of the observed variation in the index of juvenile winter run production (Martin 2000). Similarly, on the Mokelumne River, in-river spawning escapement estimates and returns to the Mokelumne River Hatchery demonstrate a highly significant positive relationship, $r^2 = 0.972$, $p<0.001$ (Miyamoto and Hartwell 1998).

The application of mark-recapture techniques beginning in 1979 provides some additional data upon which to make inferences about the quality of Feather River spawning escapement estimates. In addition to estimates of escapement, mark-recapture surveys also yield data on the number of carcasses handled and the recovery rate of tagged carcasses. Assuming relatively similar sampling efforts among years, we can expect to see certain patterns in recovery rates, the number of carcasses handled, and the resulting escapement estimate. Recovery rates should be relatively constant or perhaps inversely proportional to indices of population abundance, for example. Carcasses handled should remain relatively constant from year to year or increase with higher abundance due to the increased availability of carcasses (i.e. less search time).

Analyzing trends and mark-recapture statistics indicate that recovery rates in the LFC section are generally higher than those observed in the THERM section, averaging 46.9% and 34.4%, respectively (Figure 9). This trend reflects that the LFC is a smaller river, making it easier to search for and recover tagged carcasses. The LFC also tends to receive more sampling effort than the THERM section, which should also increase recovery rates. Overall, recovery rates demonstrate considerable inter-annual variability. One apparent trend is the increasing recovery rates observed in both the LFC and THERM sections during the 1990's. Trends in the number of carcasses handled mirrors the trends observed for recovery rates. In the LFC, a markedly larger number of carcasses were handled relative to the THERM section, averaging 13,446 and 4,562 respectively (Figure 10). A trend of increasing carcasses handled is also evident through the period of record in the LFC. However, in this case, no such pattern is evident in the THERM river section.

In analyzing patterns from mark-recapture escapement surveys, it is also useful to compare these variables to independent indices of salmon spawner abundance in the Feather River. Again, hatchery returns provide the best data set for this purpose. If hatchery returns can be expected to reflect trends in salmon abundance then we might expect to see corresponding trends in recovery rates and carcasses numbers reported from mark-recapture surveys. Lower recovery rates for example, might be associated with larger hatchery returns since the proportion of fish tagged will be a smaller proportion of the total fish available. However, a comparison of recovery rates and hatchery returns for the LFC section does not reveal an inverse relationship (Figure 11). Instead, we find a slightly positive but non-significant relationship, with a very small proportion of variation explained (2%). For the number of carcasses handled, a more expected result is attained. Carcasses handled in the LFC demonstrate a significant positive relationship with hatchery returns, $r^2 = 0.682$, $p = 0.000$ (Figure 12). However, as with earlier analysis, this trend is unduly influenced by the outlying year 2000 observation. Removing this outlying point reduces the r^2 to 0.331, but the positive relationship remains at $p = 0.025$ (Figure 13). No Comparisons were made for the THERM section because previous analysis showed it to be poorly correlated with LFC and hatchery abundance measures.

Interpreting the meaning of trends and relationships in mark-recapture statistics is difficult because of the many factors, other than salmon abundance, which may influence the observed values. Weather, water clarity, crew experience and sampling practices all can potentially influence the outcome of mark-recapture escapement estimates. Despite these limitations, this analysis of data resulting form mark-recapture escapement surveys seems to reveal some disturbing irregularities. Whatever the source of the irregularities and regardless of whether we are able to identify them in hindsight, they are significant because they are almost certainly having a profound effect on the quality of escapement data. The high variability of recovery rates observed seems to exceed that which could be expected from a study employing standardized methods, strict sampling protocols and meeting the stringent assumptions of the mark-recapture techniques. The observed recovery rates are particularly troubling in light of the known level of effort and sampling approach applied on past Feather River escapement surveys. An average recovery rate of 46.9% in the LFC implies that it was roughly this proportion of the total carcass population that was handled in some way by the survey crew. However, given that the crew worked off of one boat, did not search mid-channel areas, and had only one day to search the entire 8 mile Low Flow Channel, it is difficult to comprehend how such a recovery rate could legitimately be achieved, regardless of the number of salmon present. This point is further made by way of comparison with data from the 2000 escapement survey effort. During this survey, detailed in the following section of this report, efforts were more than quadrupled from previous years, with 2-3 boats and additional shore crews spending as many as five days surveying the river each week. Special efforts were also made to sample all areas of the river and not just near shore areas, as was the practice previously. Despite these Herculean efforts, the 2000 survey achieved only a 57% recovery rate in the LFC and a 20% recovery rate in the THERM section. The 2000 recovery rate for the THERM section is the third lowest in the history of the survey. Collectively, these findings suggest that past salmon spawning escapement surveys followed inadequate sampling protocols that very likely produced error prone and badly biased escapement estimates.

Year 2000 Salmon Spawning Survey

In Fall 2000, DWR and DFG cooperatively conducted an intensive escapement survey on the Feather River. The survey was based on the same basic premise of earlier carcass mark-recapture performed on the Feather River since 1979, however the year 2000 study increased effort, followed a more rigorous set of sampling protocols, and collected information on a finer spatial scale. In addition to obtaining an accurate estimate of spawning escapement, the year 2000 survey sought to collect detailed information about the spatial and temporal distribution of spawning salmon, pre-spawning mortality among female salmon, and size and sex distribution of the spawning population. The survey also served to provide a sound sampling design for collecting coded wire tagged (CWT) salmon.

Methods

The survey area consisted of two eight mile river segments, the Low Flow Channel (LFC) and the Lower Reach (LR). The LFC was divided into four sections each covering approximately two river miles. River sections within the LFC were further divided into units consisting of a single riffle/pool sequence (see Figure 14 for example). The LR segment was divided into three sections, but was not subdivided into individual riffle/pool units. Sparse data in the LR made it necessary to group the data from the LR sections into one, referred to as Section 5.

Mark-recapture experiments on salmon carcasses were conducted weekly from September 5 through December 14. "Fresh", non-CWT carcasses were marked with individual numbered tags and placed back into the river. Additional data collected on fresh fish included: section recovered, fork length, sex, age, egg retention (females only) and release criteria (i.e. shallow or deep, sink or float). Egg retention or pre-spawning mortality was determined by assessing female carcasses for the quantity of eggs remaining. Untagged, non-fresh carcasses were checked for tags that may have been placed in previous weeks, counted, and removed from the experiment by chopping the fish in two with a machete.

Population estimates were generated using the Schaefer mark-recapture model. Detailed collection of mark-recovery data in the LFC allowed us to make population estimates for individual units (representing a single riffle-pool sequence) or grouped over an entire river segment. This analytical flexibility made it possible to perform a bootstrap re-sampling exercise in which different sampling strategies and levels of sampling effort could be evaluated for their effect on the overall population estimate for the LFC river segment. Our re-sampling simulations were based on nine levels of effort (5, 10, 15, 20, 25, 30, 35, 40, and 44 units surveyed) and three different sampling strategies (near shore only, mid-channel only, and both).

Simulations were conducted in the following manner. The carcass survey database was queried to restrict available data to the desired sampling strategy (near shore only, mid-channel only, or both). Next, river units corresponding to the level effort (5, 10, 15, 20, 25, 30, 35, 40, or 44) were selected at random from the database. Data from the units selected were then pooled and an overall population estimate generated.

This process was then repeated for one-thousand iterations at each level of effort, this allowed us to assess variance in estimate for each level of sampling effort.

Results

Sex Distribution

The proportion of males and females encountered in carcass survey varied through time and between river sections. Females were almost always more abundant than males, outnumbering them by more than two to one in some weeks (Figure 15). Females also appeared to be most abundant during the middle period of the survey, and less so at the tails of the survey period (Figure 15). Female salmon also tended to be more abundant in upstream river sections than they were in downstream river sections (Figure 16). The most downstream area sampled (section 8) was the only river section where males salmon outnumbered female salmon (Figure 16).

Pre-spawning Mortality

The occurrence of pre-spawning mortality among females changed sharply through time, but showed less variation between river sections. In all river sections, from 100% to 80% of all female carcass sampled in the first three weeks had died before spawning any eggs (Figure 17). Pre-spawning mortality decreased after this initial period however, and stayed well below 40% for most weeks and river sections (Figure 17). The overall average spawning success was 58%. One of the few differences evident between river sections is the earlier increase in spawning success among salmon in sections 1 and 2 (Figure 17).

CWT Distribution

Out of 6,224 carcasses checked only 205 CWT tagged salmon were recovered. Coded wire tag (CWT) recoveries were distributed irregularly through the survey period. In all river sections, the proportion of CWT carcasses was much higher in the first five weeks of the survey than in latter weeks (Figure 18). Interestingly, CWT recoveries reached some of their highest levels in the last week of the survey for sections 3 and 4 (Figure 18).

Size Distribution

A total of 6,244 carcasses were measured. Mean fork length for male salmon was 87.2 cm, and ranged in size from 34 to 120 cm. Female salmon averaged 81.7 cm fork length, and ranged in size from 49 to 107 cm. Length-frequency plots demonstrate further differences in size distribution among male and female salmon (Figure 20). Males were generally larger than females, but also expressed a greater range of sizes (Figure 20). The male length-frequency distribution also reveals a weak bimodal distribution, with a second peak corresponding to smaller grilse, 2 year-old salmon (Figure 20). Female salmon demonstrate a more compact fork length distribution (Figure 20).

Population Distribution and Estimation

The total fall run chinook, in-river, spawning escapement estimate for 2000 was 117,824. Over the fifteen week survey, 6,244 fish were tagged, and another 44,328 were counted, checked for tags and chopped. The majority of salmon (63% or 74,315) spawned in the LFC (Table 1). 43,509 salmon are estimated to have spawned in the river segment downstream of the Thermalito Outlet, this number represents 37% of the total population estimate (Table 1). Salmon spawning was evenly distributed among the first three sections of the LFC, but was significantly less in LFC section 4 (Table 1).

The temporal distribution of carcasses indicates that spawning occurred from early September through mid-December (Figure 21). Spawning in the LFC peaked in mid-October (Figure 21). The temporal distribution of spawning in the LR differed dramatically from the distribution in the LFC. In the LR, spawning lagged slightly behind activity observed in the LFC (Figure 21). In contrast to the LFC, spawning in the LR did not show any clear peak of abundance. Instead, LR spawning plateued at roughly 4000 salmon per week, and did not drop appreciably until late November (Figure 21).

TAGGED CARCASS MOVEMENT

One of the ancillary benefits of recording data on a fine spatial scale and using individually numbered tags is that it becomes possible to assess the distance carcasses move from the location where they are tagged and released. Analysis suggests that most carcasses (60%) are recovered in the same unit where they were tagged and released (Figure 19). 80% of tagged carcasses are recovered within three units of the unit where they were released (Figure 19).

SIMULATION STUDY

Population estimates varied considerably with different levels of sampling effort (number of river units surveyed) and sampling strategy. For each of the three sampling strategies, the mean population estimate increased up to an asymptote representing full sampling effort (Figure 22). For near shore and mid-channel sampling this asymptote occurs at 74,315, the complete escapement estimate for the LFC. Mid-channel only sampling yields an asymptote equivalent to approximately 42,000. Near shore only sampling yields an asymptote equivalent to approximately 31,000. Variability in escapement estimates also decreased as sampling effort increased (Figure 22). At all levels of effort, average population estimates were progressively lower from near shore and mid-channel sampling, to mid-channel only sampling, to near shore only sampling.

Discussion

In light of the large numbers of spawning salmon in the Feather River and the generally poor quantity and quality of spawning habitat, we expected to find pre-spawning mortality coincident with the timing of spawning activity. Instead, we found that pre-spawning mortality was highest very early in the survey, well before the peak of spawning activity, and gradually attenuated through out the study period. This trend suggests that competition for limited spawning habitat was not the primary factor driving successful spawning. Pre-spawning mortality observed in the early weeks of the survey may instead result from fishing pressure, or physiological stress associated with upstream migration. However, the overall average pre-spawning mortality rate of 42% is much higher than the 4 to 13% observed among Fall-run chinook on the Sacramento River (Snider, Reavis and Hill 1999). The relatively high rates of pre-spawning mortality on the Feather River may stem from some combination of heavy angling pressure and stressful river conditions.

The relatively high representation of Coded Wire Tagged (CWT) salmon early in the spawning period suggests that hatchery fish tend to arrive early, and that perhaps, wild salmon tend to arrive later. However, this trend may also be the consequence of sampling artifacts, such that the likelihood of noticing and recovering a CWT salmon is inversely proportional to the number of salmon present. Another fact that calls into question the validity of the collected CWT data is the relatively small proportion of CWTs that were recovered relative to the number of salmon checked. Only 205 CWT salmon were recovered, which composes roughly 3% of the over 6,000 salmon checked. Since approximately 15% of the production at Feather River Hatchery is tagged, each tagged fish should represent approximately 7 hatchery origin fish. Based on this calculation, we conclude that hatchery fish represented only 24% of the observed spawning population; a number so low that it is scarcely believable.

The fact that CWT recoveries were surprisingly rare and unevenly distributed (spatially and temporally) has important management implications, particularly for efforts to analyze and interpret CWT recovery data. For example, efforts to expand CWT recoveries and estimate year-class contribution rates could be badly based if CWT sampling programs do not account for the decidedly non-random distribution of CWT within a given salmon population. Expansions will be similarly biased if existing sampling programs under-count CWT recoveries.

The year 2000 spawning escapement survey estimated a total in-river, spawning population of 117,824 salmon. This is the highest spawning escapement ever reported on the Feather River. It is a clear outlier among estimates from all other years. Since the year 2000 survey employed greater effort and a detailed sampling protocol, it is difficult to compare this estimate with the previous estimates, where effort and sampling protocols were poorly documented.

One trend that is consistent with recent spawning escapement surveys is the relative distribution of spawning between the LFC and the Feather River below the Thermalito Outlet. The year 2000 survey found that most (63%) of salmon spawned in the LFC. This trend seems to suggest that habitat in these sections is more suitable for spawning and therefore more attractive to spawning salmon. However, this pattern may also reflect an affinity for river sections near the hatchery. This attraction could be based upon a genetic tendency among hatchery fish to return near as possible to the point of origin, or a chemical cue that attracts salmon regardless of their origin. Whatever the explanation, the intensity of spawning in the LFC is troubling since the LFC represents a small proportion of the available spawning habitat relative to the river below the Thermalito Outlet. The timing of salmon spawning was also notably different between the two river segments. Spawning downstream of the Thermalito Outlet did not show a distinct peak and extended later than that observed in the LFC. The explanation for this trend is unclear, but it could represent a distinct and possibly more "wild" component of the Feather River fall-run salmon population.

One of the principal problems with most of California's salmon spawning escapement surveys is the absence multiple techniques for verifying the validity of escapement methods (UC Davis, June 22, 2000). Since alternative sampling programs for measuring escapement are expensive and difficult to implement, simulation modeling represents a sound, interim approach. The detailed collection of mark-recovery data in the LFC made it possible to simulate some different types of sampling effort and strategies to examine how they might effect final escapement estimates. An objective of these simulations was to test the validity of the assumption of equal catchability, upon which mark-recapture carcass surveys are based. Equal catchability implies that every carcass in the river has the same probability of being recovered (found by survey crews) regardless of whether it is tagged or not. In other words, the carcasses to be found need to be randomly mixed, *or* alternatively, the process by which they are recovered must select the carcasses at random from those available. If this assumption is met, then the simulations should demonstrate that differences in sampling effort or strategy do not bias escapement estimates. However, this is not the case. Simulation results clearly show a strong negative bias for both sampling effort and sampling strategies that do not include all river areas.

This bias results from a systematic violation of the assumption of equal catchability. Carcass mark-recapture studies have an inherent tendency to violate this assumption because salmon carcasses are dead, and therefore do not exhibit the mixing behavior expected from typical mark-recapture conducted with living animals. Mark-recapture techniques for estimating populations where not designed nor intended for use on dead animals. Since the tagging of inanimate objects is not a common practice among purveyors of mark-recapture techniques, the validity of the approach has received little critical review.

Despite the lack of pertinent literature on the subject, a simple analysis of typical salmon carcass distribution patterns and common sampling designs indicates that there is cause for serious concern. Validity of carcass mark-recapture requires that at least one of two potential premises on the distribution and sampling of carcasses be true. Premise One assumes a pool of carcasses is randomly distributed throughout the river. Since these carcasses are always distributed at random, samples could be drawn by any design (random, systematic, haphazard) and the resulting data would always be valid. Figure 23 provides a schematic example of what this distribution and the resulting sampling might look like. Premise Two assumes that carcasses are instead patchy in their distribution and that little mixing occurs between clusters of salmon carcasses. In this case, the distribution of carcasses is decidedly non-random. Obtaining valid data in this circumstance requires randomized sampling. Unfortunately, truly randomized sampling among carcass surveys is virtually unknown. A more typical sampling program is depicted in Figure 24. Here, surveys crews skip from one salmon cluster to another, often skipping clusters to save time or skipping clusters that are inaccessible (due to depth, clarity or obstacles).

Of the two premises considered, Premise Two seems to provide the more realistic model of how carcasses are typically distributed in the field. Indeed, field observations and data analysis both suggest that the carcass population is composed of many, small, unmixed sub-populations of carcasses, rather than by one panmictic population, as many carcass surveys implicitly assume. While some drift and mixing undoubtedly occurs between carcass clusters, our tracking of individually marked carcasses indicates that the vast majority of carcasses travel relatively short distances before settling out of the current. This mixing occurs primarily in the longitudinal dimension however (upstream-downstream), it is highly unlikely that any lateral mixing of carcasses occurs. This is an important observation since many carcass surveys cover only one side of the river at a given sampling location.

Results of our carcass survey simulations also support Premise Two. If significant mixing did occur between cluster of salmon carcasses then we would expect to find variance around the true escapement estimate rather than a pervasive negative bias for all levels of sampling effort below full sampling (i.e. all units, all channel areas). Indeed, each unit or carcass cluster on the river seems to represent its own distinct sub-population. Sampling that overlooks any one of these clusters for any reason (e.g. inaccessibility, insufficient time, sampling design) is effectively leaving that component of the population out of the final estimate and inducing a negative bias.

In light of these results, a question arises: What is the appropriate sampling design and level of effort to use in a carcass mark-recapture survey? The ideal sampling design would allow individual carcass to be selected at random from the total population of

Well this assumes we know all the carcasses before sampling

carcasses. However, this type of sampling is problematic because carcasses cannot be selected at random from areas where carcasses are inaccessible (too deep, too swift, no wading or boat access). Yet, even in areas that can be surveyed, there is no practical means by which a random subset of carcasses could be selected from the total available. Compounding the problem is the fact that survey crews are routinely faced with limited time and a large area or number of carcasses to deal with. Faced with these limitations, crews often resort to getting the most carcasses for their effort; focussing on areas easily searched and with large concentrations of carcasses and ignoring less friendly parts of the river. While this type of sampling strategy clearly violates the assumption of equal catchability, it is probably common to many surveys simply because, under the circumstances, it is very difficult to sample otherwise.

The second best, but more practical approach may be to simply apply effort and sampling protocols that specifically require all river areas to be sampled. This method also requires careful planning and attention to detail among the survey crew. However it was successfully applied in the year 2000 Feather River carcass survey with favorable results. Whether by design or necessity, this is the sampling strategy that is typically employed on small rivers, where accessibility is not a problem, and where salmon runs are typically manageable in size. In fact, the only published studies which have attempted to test the validity of carcass mark-recapture, occurred on Bogus Creek, a small tributary to the Klamath River. These studies found that carcass mark-recapture, analyzed with various competing statistical models, yielded estimates comprable to weir counts for the same period (Skyes and Botsford 1986, Boydstun 1994,). While these favorable results probably do not extend to larger rivers (for reasons identified previously), they suggest that when all areas of the river are sampled completely, or close to completely, reasonably accurate estimates can be achieved. However, the level of effort required to achieve complete sampling is significantly greater than most surveys currently employee.

Irrespective of problems associated with sampling design and the distribution of carcasses, the level of effort applied on the river (crew/hours) alone can be a huge factor influencing the accuracy of resulting escapement population estimates. A simulation study conducted by Law (1994) showed that under typical conditions, and with all assumptions met, the proportion of the population surveyed had a large effect on the deviation of estimates from the true population values (Table 2). According to his work, at least 60% of the carcass population must be sampled in order to achieve an escapement estimate that is within 35% to 25% of the true value. Unfortunately, this level of effort is very difficult to achieve on all but the smallest and most easily accessible rivers, with low to moderate numbers of salmon. Most carcass surveys on large rivers of the Central Valley have catch rates that are probably from 5 to 20%. To address the problem of sampling effort, the 2000 carcass survey on the Feather River has nearly quadrupled effort from previous years (with as many as 600 field staff hours/week), and yet the overall catch rate appears to have remained under 50%.

Recommendations

Management, conservation and restoration of California's salmon stocks rest heavily upon data collected through spawning escapement surveys. In light of the significance of this information, a thorough critique and re-evaluation of survey methods and protocols is warranted. Currently we are lacking a coherent or documented statewide plan detailing the design or protocols for collection of data related to inland salmon escapement. The primary goal of any review process should be to design a sampling program which would meet the needs of management and address the issues identified here.

In the spirit of this review, the following preliminary recommendations are offered as means of immediately improving the quality of spawning escapement survey data. Many of these items have already been implemented successfully on the Feather River, and should be considered for other Central Valley salmon rivers as well.

1) Carcass mark-recapture is a technique best suited to small, easily accessible streams. The technique can also yield fairly accurate population estimates on rivers with large salmon runs, but only when the study is designed carefully and when sufficient effort is applied. Conducting reliable carcass surveys on rivers with large salmon runs or with many areas that cannot be searched effectively may prove impractical. In these instances, spawning escapement should be estimated by other means, such as direct counts from weirs and/or hydroacoustics.

2) Where carcass mark-recapture is still used, the following considerations are necessary:

- The sampling program must be designed, documented, implemented and *supervised* in the field by scientists with a thorough understanding of the theoretical underpinnings and pitfalls of the method. All crew members should be trained in these areas also.
- Take precautions to minimize violation of the assumption of equal catchability. These precautions would include instructing crews to collect samples from *all* areas of the river (including deep waters or mid-channel areas) and not just particular accessible locations or hot spots. This goal is best achieved by stratifying the river into numerous sections (riffle-pool units or smaller) prior to conducting field work.

- Provide each survey with sufficient crews and tools to do the job properly. These would include boats, long handled spears (10-20 ft) and gaffs, and tagging equipment.
- Increase survey effort on the river. For typical Central Valley rivers, there is no point of diminishing returns with carcass survey effort. Law's simulation study (1994) suggest that population estimates do not become reliably accurate until catch rates approach 60%.
- Collect data on as small a spatial scale as possible, rather than grouping information for large river segments. Collecting data on a smaller spatial scale (individual riffle-pool units or smaller) forces crews to distribute their effort on the river and provides a means of tracking distribution and recovery patterns that are biologically relevant or which could bias population estimates.
- Perform experiments and collect data such that tests can be performed on potential violation of assumptions. Double tagging, using individual tags, recording release location or release conditions all provide valuable information that can be used to assess the validity of escapement estiamtes.
- Follow a rigorous, well-designed and documented protocol that enforces all of the above mentioned items.

3) Coded Wire Tag recoveries need to:

- Become a high priority and equal focus of carcass survey efforts.
- Follow design protocols, implemented and supervised by scientists with a thorough understanding of the significance of CWT collection and the theoretical

underpinnings and pitfalls associated with the collection and interpretation of CWT data. All crew members should be trained in these areas also.

- Make collections on a systematic or random basis over the entire study area and covering the entire study period. Spot sampling at particular time or location could result in badly biased CWT data.
- Record associated information about collections, includ~~ed~~ing which areas where searched and when. Each recovery should include details about where and when the sample was acquired.
- Consider alternate collection strategies. Such as having a separate crew responsible specifically for weekly sampling and collection of CWTs. Perform random sub-sampling for CWT at weirs or other direct count facilities (if they become available)

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Miyamoto, J.J. and R.D. Hartwell. 1998. Population trends and escapement estimation of Mokelumne River fall-run chinook salmon (Oncorhynchus tshawytscha). East Bay Municipal Utility District.

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Feather River Fall Run Spawning Escapement, 2000

Section	River Mile	From	To	Population estimate	% of LFC total	% of grand total
1	67 to 65.5	Fish Barrier Dam	Hwy 70 Bridge	20841	28	18
2	65.5 to 63	Hwy 70 Bridge	Great Western	23808	32	20
3	63 to 61	Great Western	Steep Riffle	20202	27	17
4	61 to 59	Steep Riffle	Thermalito Outlet	9464	13	8
5	59 to 51	Thermalito Outlet	Gridley Bridge	43509		37
			LFC total	74315	100	63
			grand total	117824		100

Table 1

Schaefer Model	Catch Rate (proportion of the population surveyed)			
	10-20%	20-40%	40-60%	60-90%
Mean % deviation from true population value	+80 to 70%	+70 to 50%	+50 to 35%	+35 to 25%

Table 2. ~~Figure~~ . Summary of carcass mark-recapture simulation results from Law (1994). Results show large bias in population estimates occuring at various levels of effort. The Schafer Model is the most commonly applied method for estimating salmon escapement in California, and was one of several models tested by Law.

Table 2

Fig 1

Feather River Fall Run Salmon

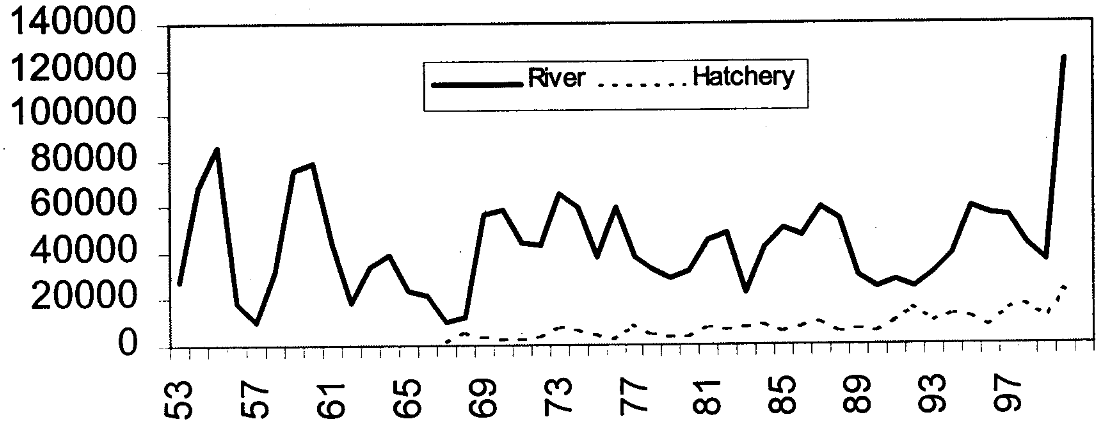
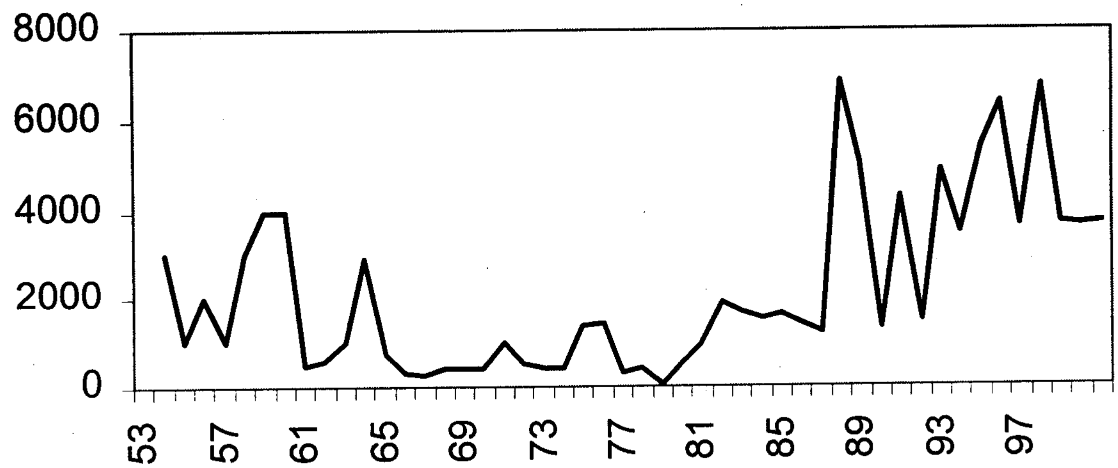


Fig 2

Feather River Hatchery Spring Run Returns



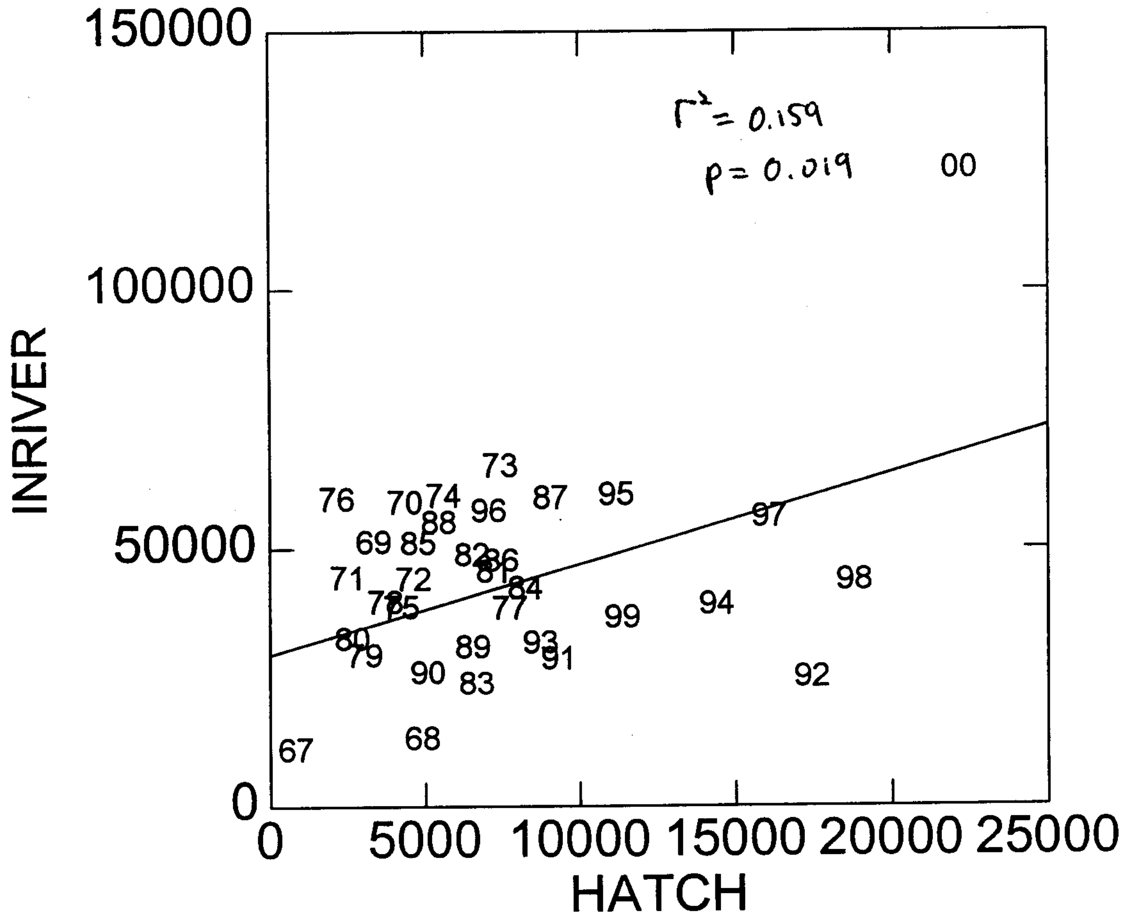


Fig 3

Total in-river fall run estimate vs. hatchery returns.

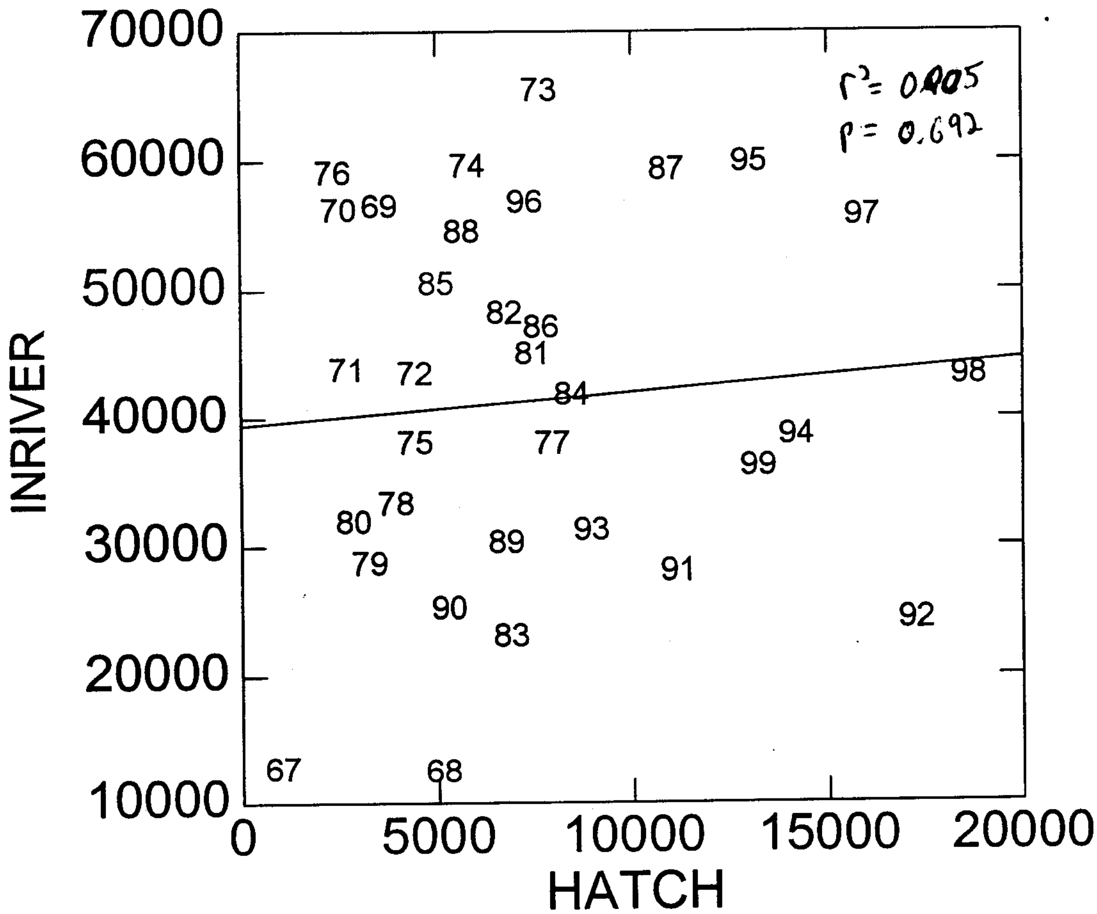


Fig. 4

Total in-river fall-run w/o y2000 vs. hatchery returns.

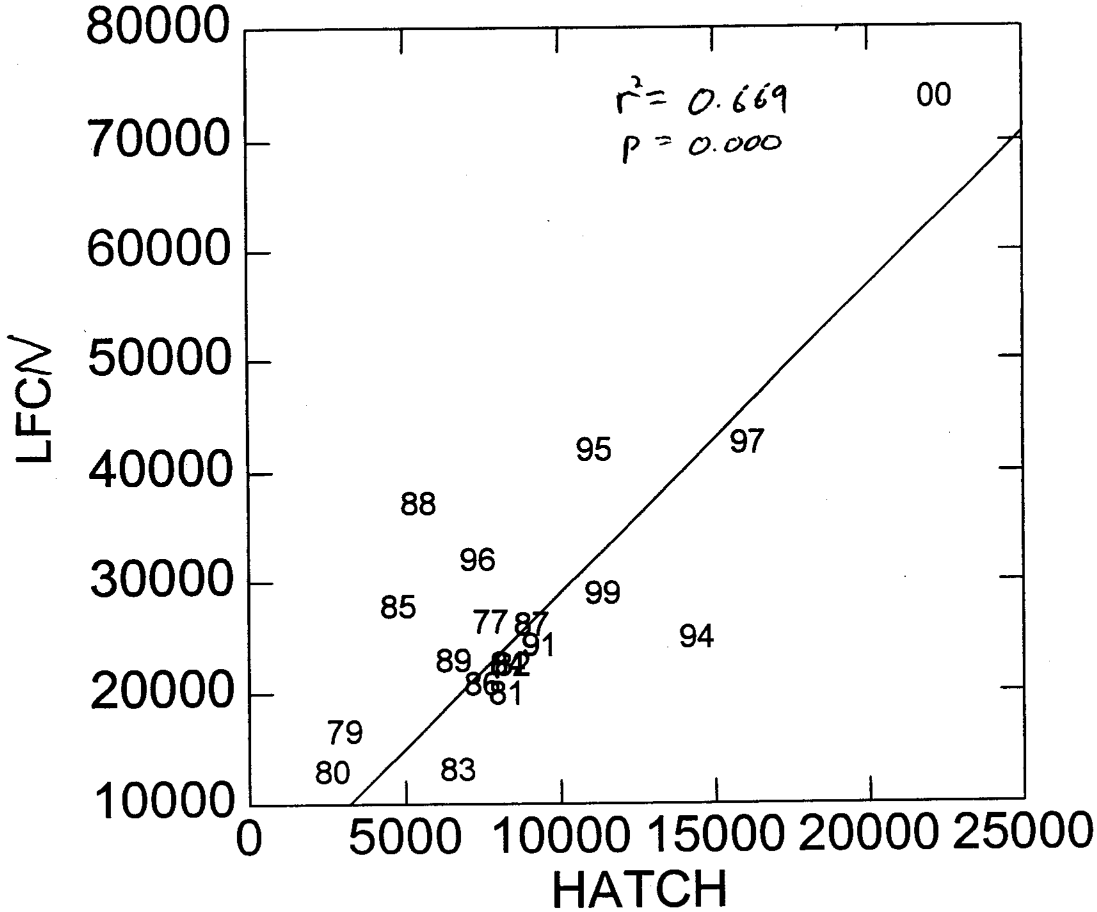


Figure 5

Low Flow Channel in-river escapement vs hatchery returns

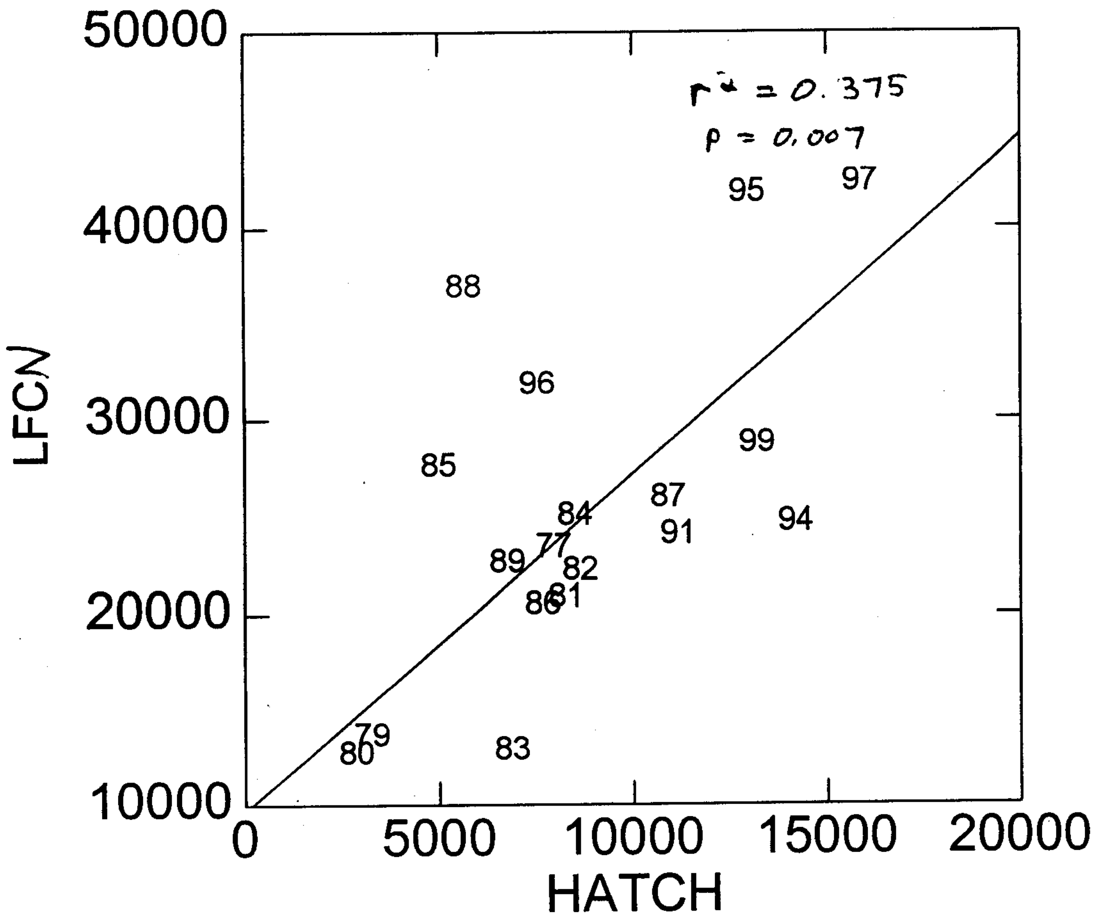


Figure 6
LFC in-river escapement
vs. hatchery returns
w/o Y2000

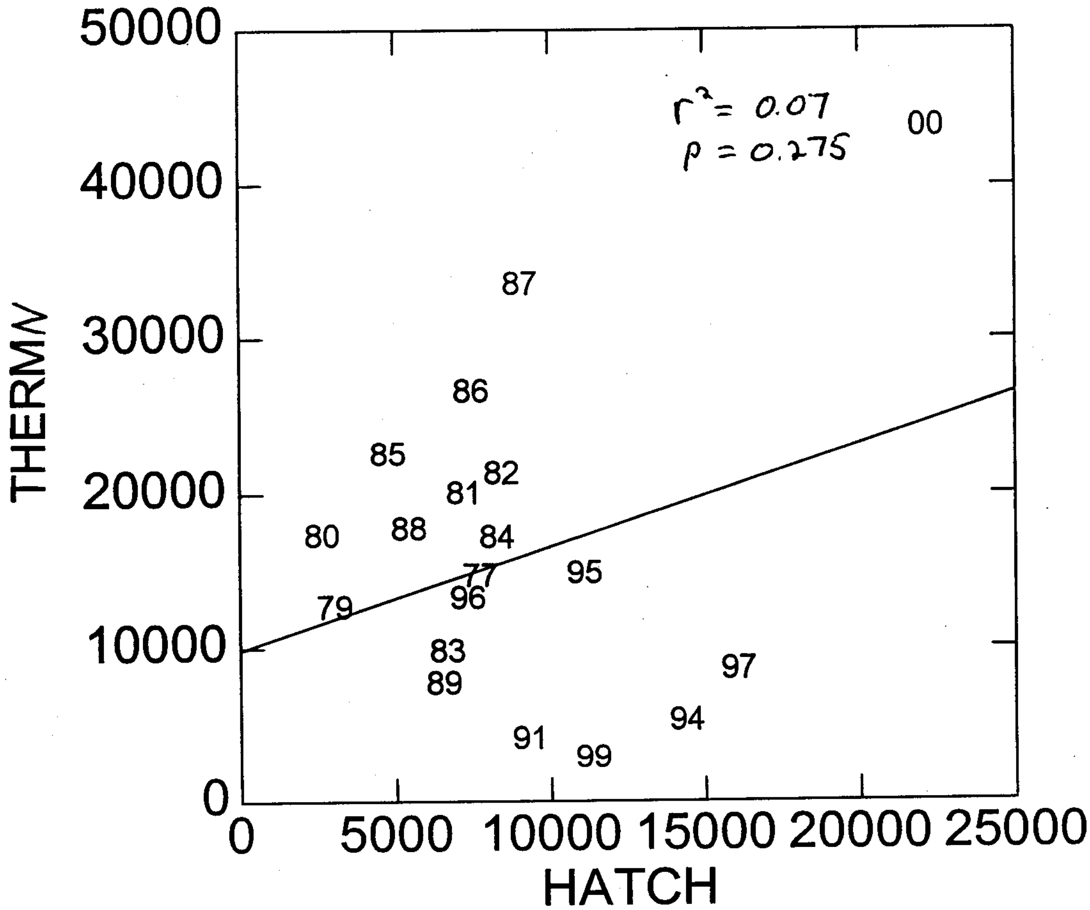


Figure 7
Therm escapement
vs hatchery returns

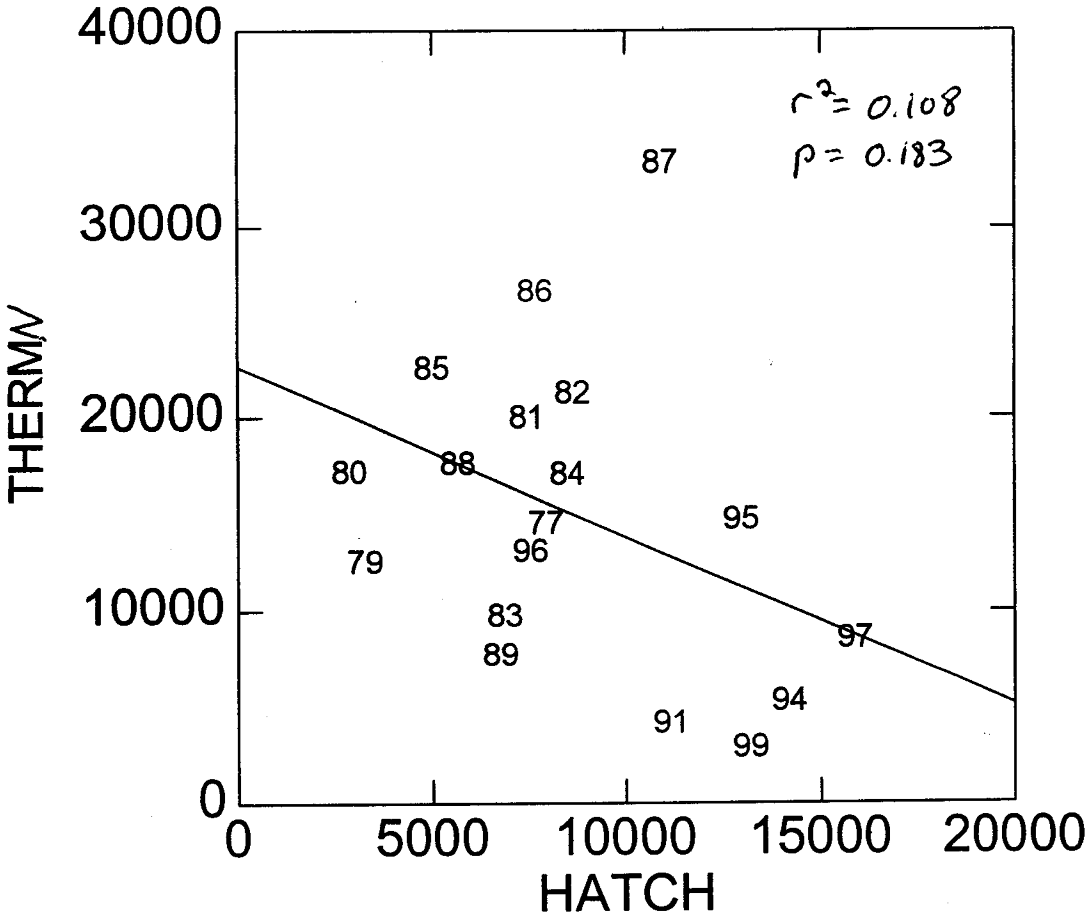


Fig. 8

THERM escapement estimate vs. hatchery return. w/o Y2000

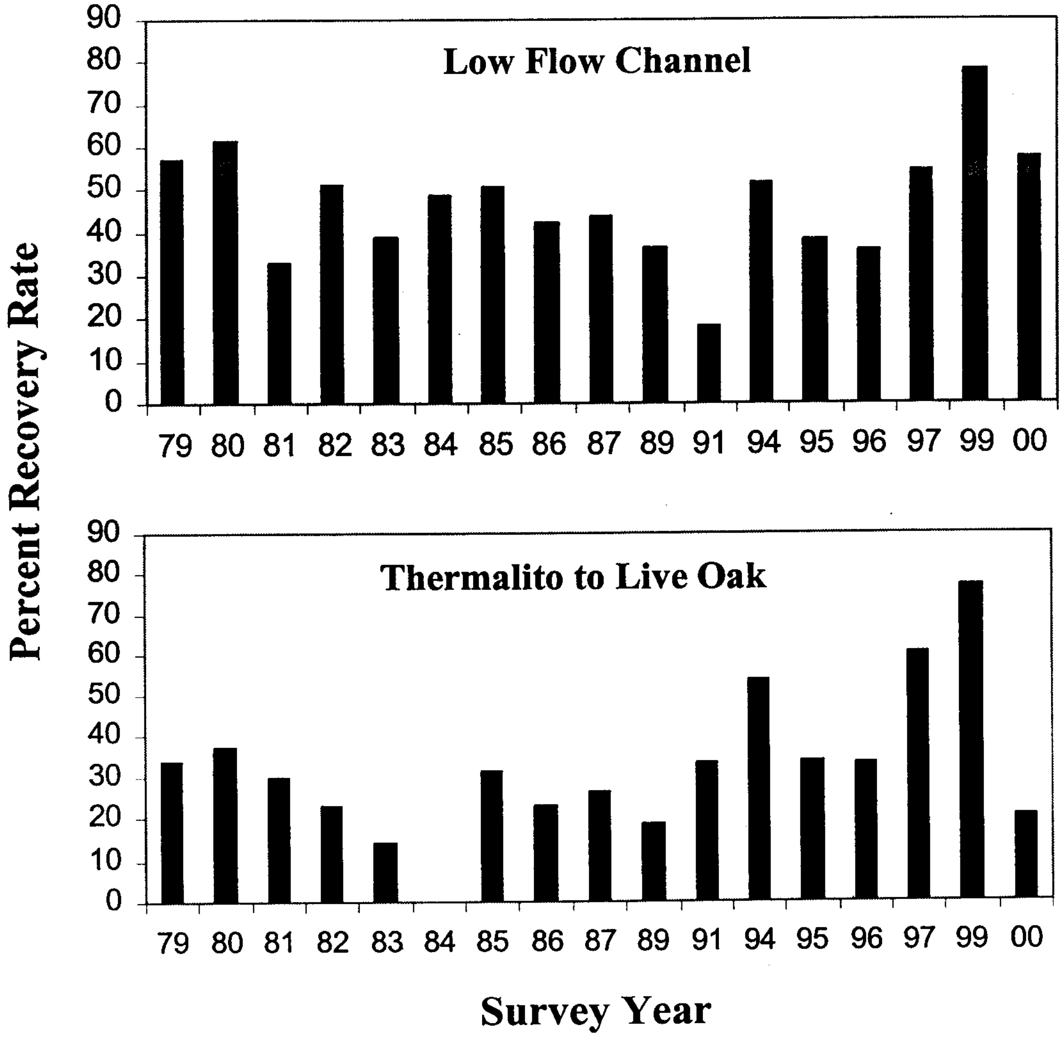

Low Flow Channel
Thermalito to Live Oak
Percent Recovery Rate
Survey Year
0
10
20
30
40
50
60
70
80
90
79
80
81
82
83
84
85
86
87
89
91
94
95
96
97
99
00

Fig. 9

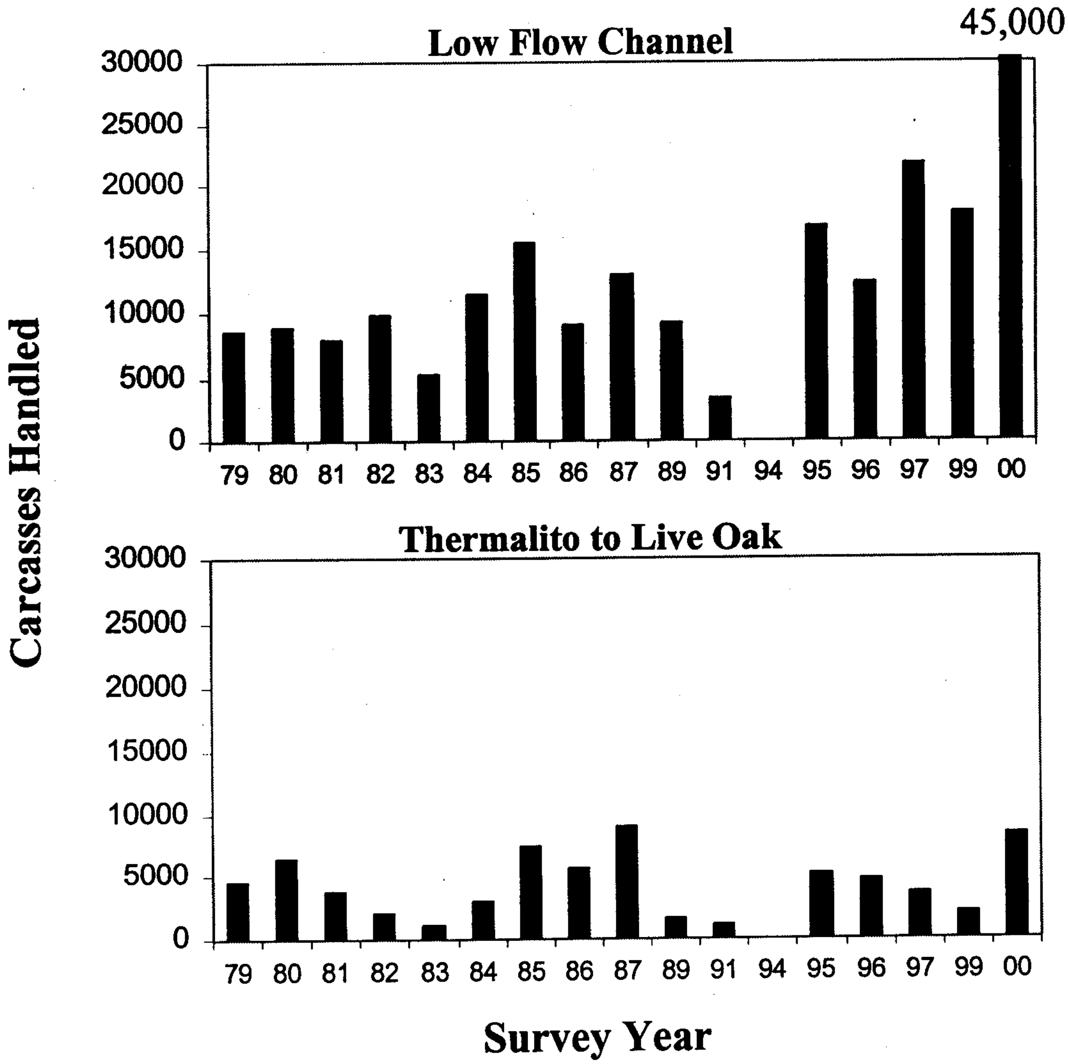

45,000
Low Flow Channel
Thermalito to Live Oak
Carcasses Handled
Survey Year
30000
25000
20000
15000
10000
5000
0
79 80 81 82 83 84 85 86 87 89 91 94 95 96 97 99 00

Fig 10

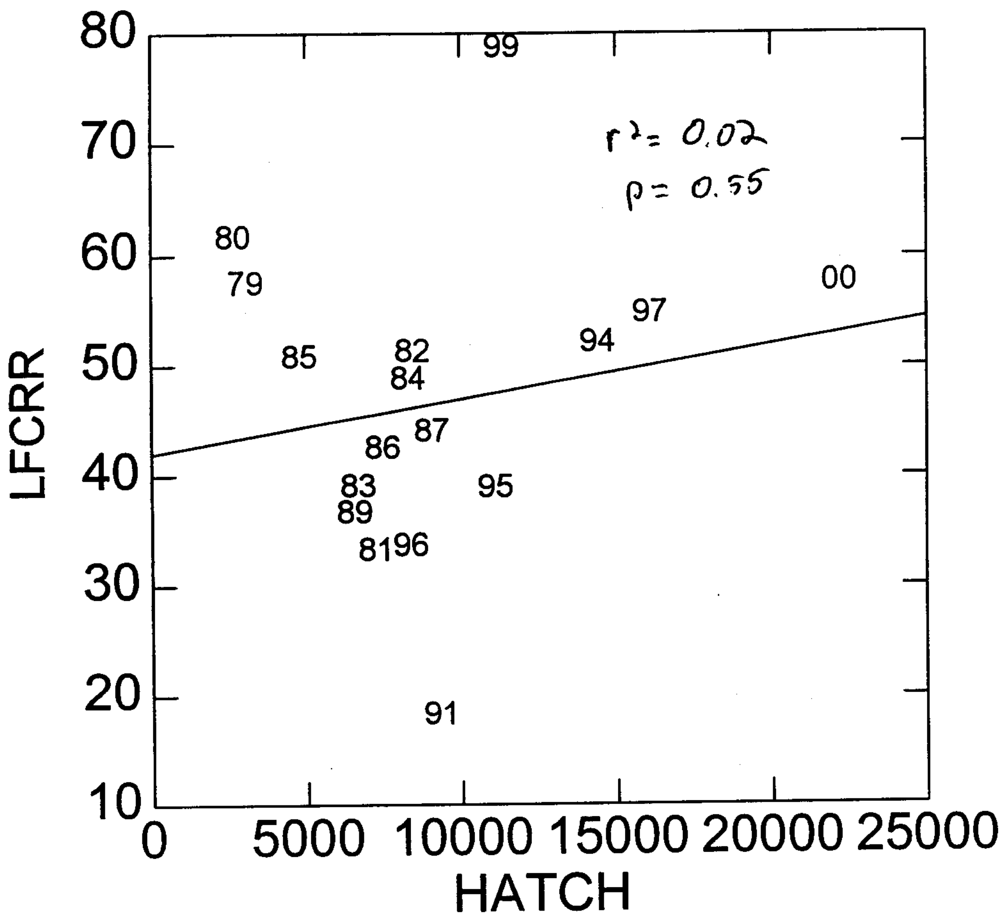
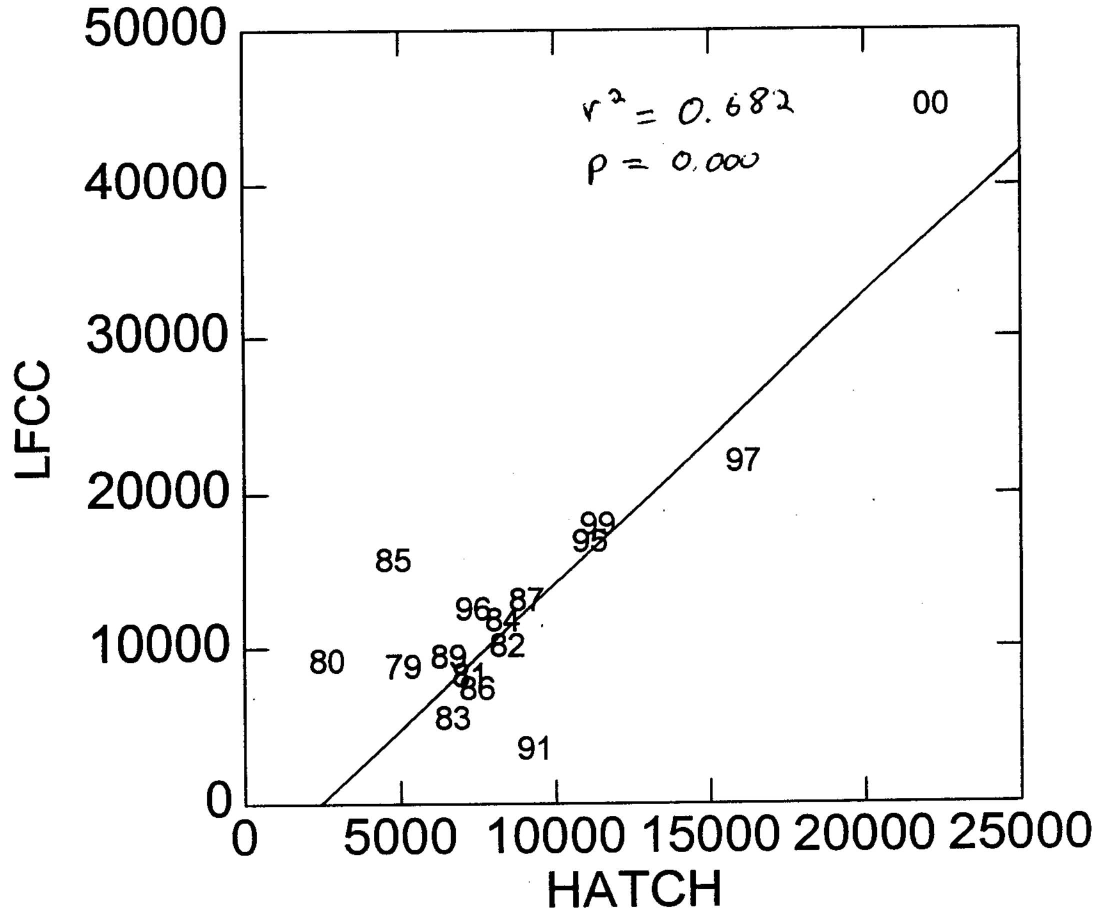
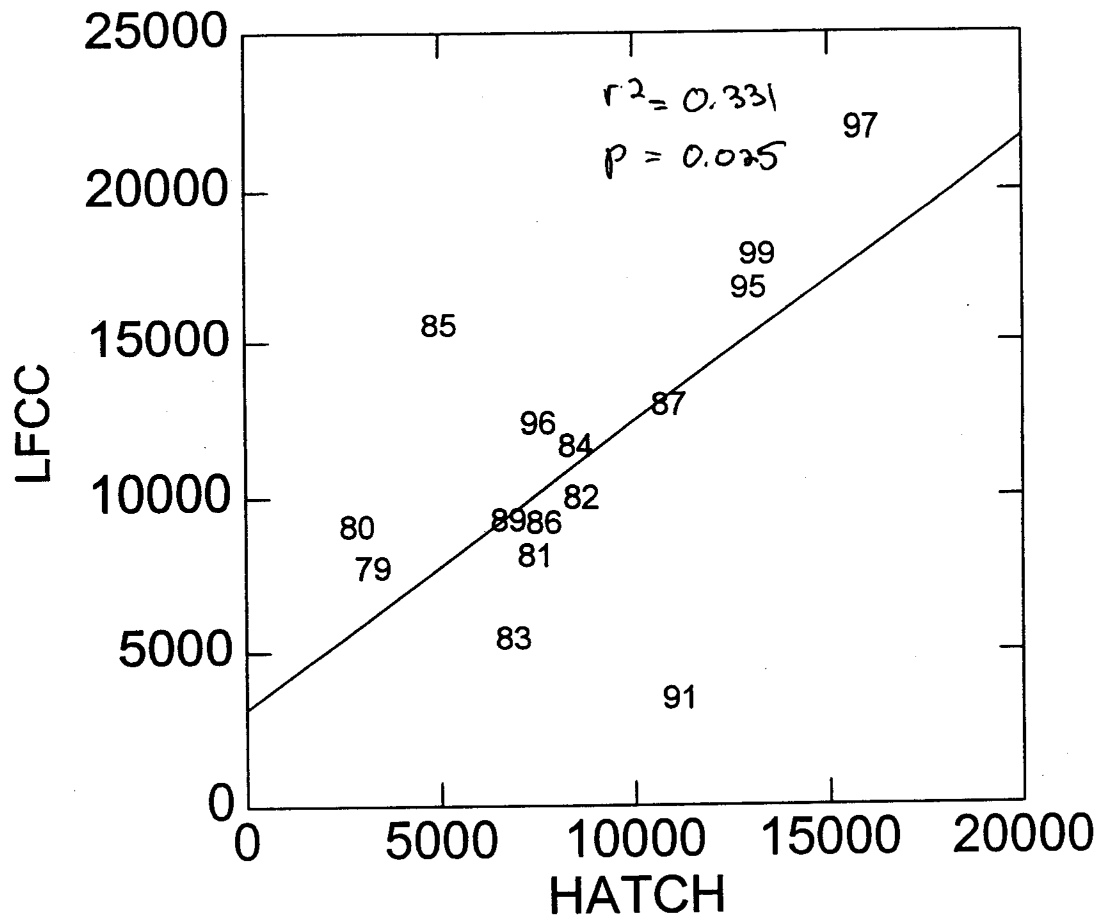

80
70
60
50
40
30
20
10
LFCRR
0
5000
10000
15000
20000
25000
HATCH
99
r² = 0.02
p = 0.55
80
79
00
97
94
85
82
84
87
86
83
95
89
8196
91

Figure 11



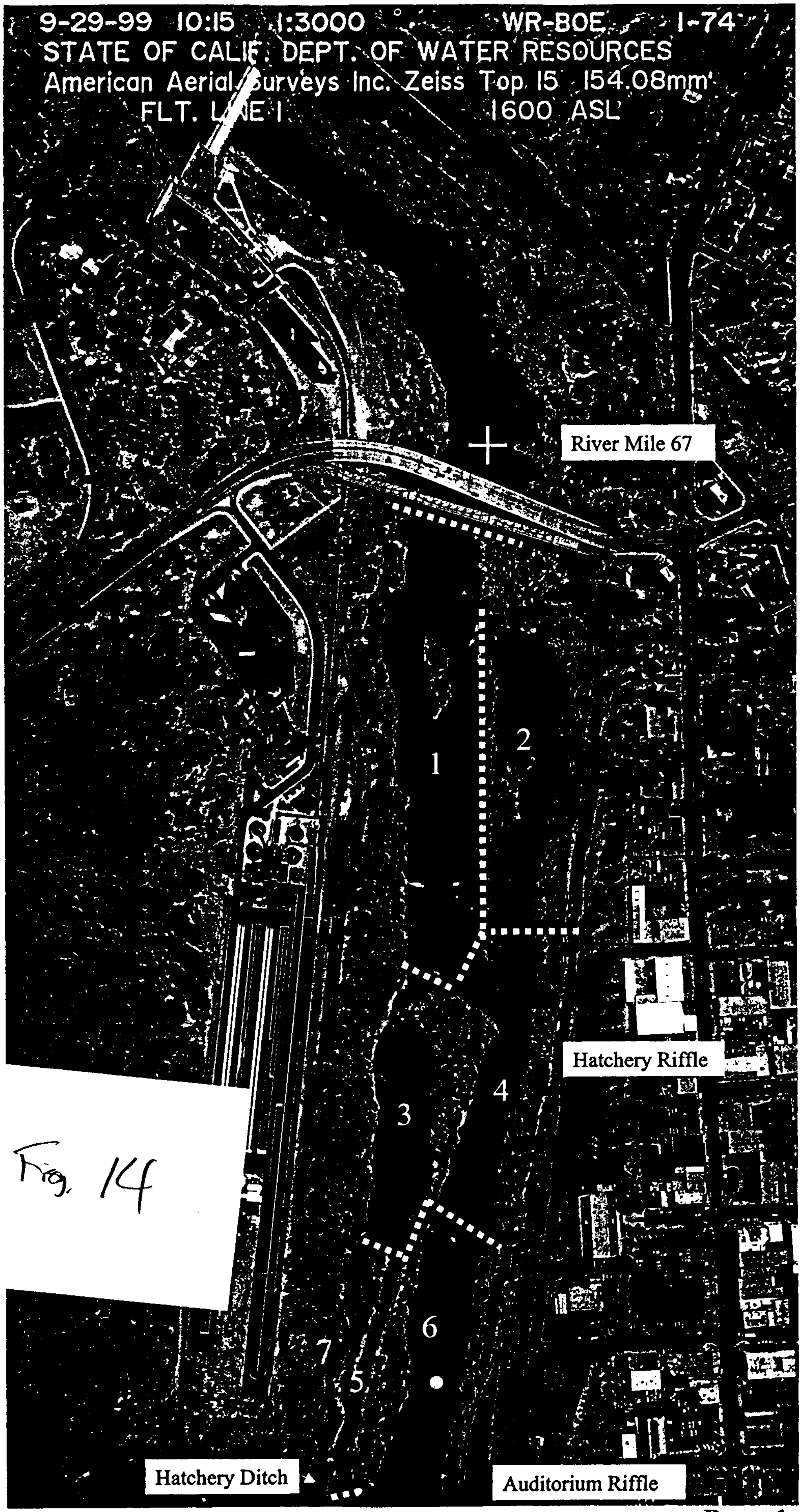
$r^2 = 0.682$
$p = 0.000$
LFCC
HATCH
00
97
99
95
85
96
87
84
82
80
79
89
81
86
83
91
0
10000
20000
30000
40000
50000
5000
15000
25000

Figure 12



$r^2 = 0.331$
$p = 0.025$
25000
20000
15000
10000
5000
0
LFCC
0
5000
10000
15000
20000
HATCH
97
99
95
85
87
96
84
82
80
89
86
81
79
83
91

Figure 13


9-29-99 10:15 1:3000 WR-BOE 1-74
STATE OF CALIF. DEPT. OF WATER RESOURCES
American Aerial Surveys Inc. Zeiss Top 15 154.08mm
FLT. LINE 1 1600 ASL
River Mile 67
1
2
Hatchery Riffle
3
4
Fig. 14
6
7
5
Hatchery Ditch
Auditorium Riffle

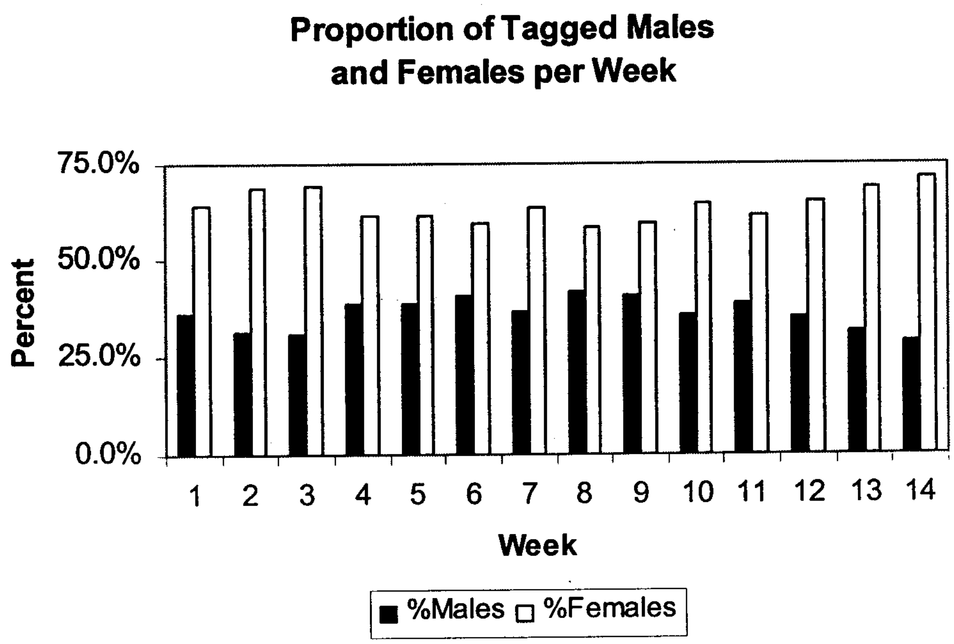

Proportion of Tagged Males
and Females per Week
75.0%
50.0%
25.0%
0.0%
Percent
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Week
%Males
%Females

Fig. 15

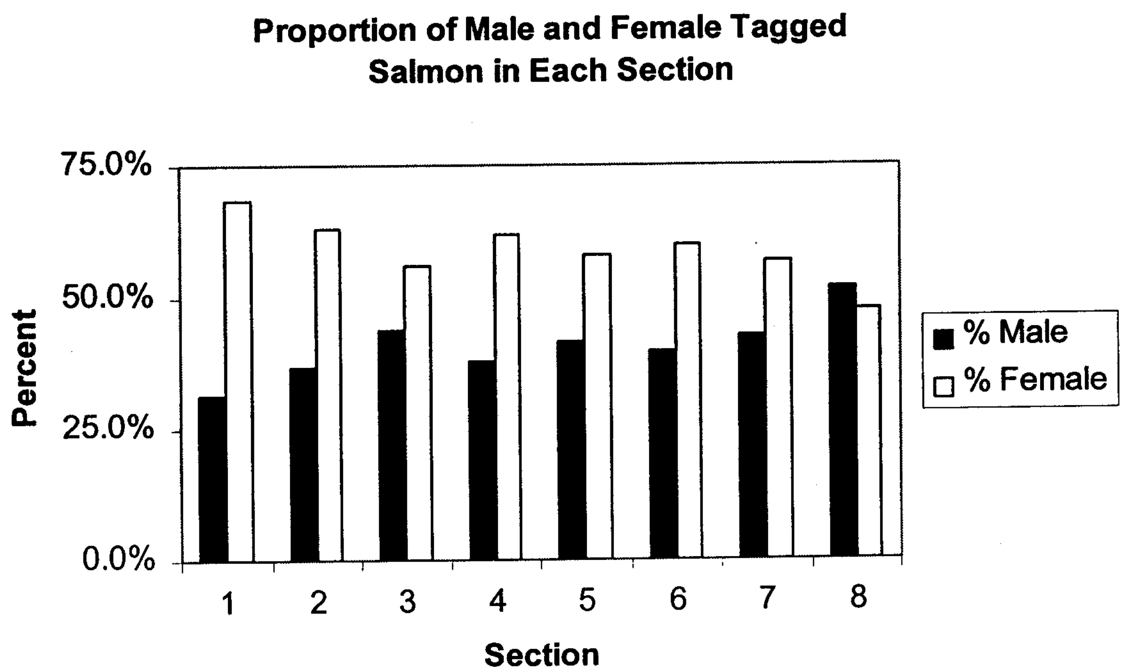

Proportion of Male and Female Tagged
Salmon in Each Section
75.0%
50.0%
25.0%
0.0%
Percent
1
2
3
4
5
6
7
8
Section
% Male
% Female

Fig 16

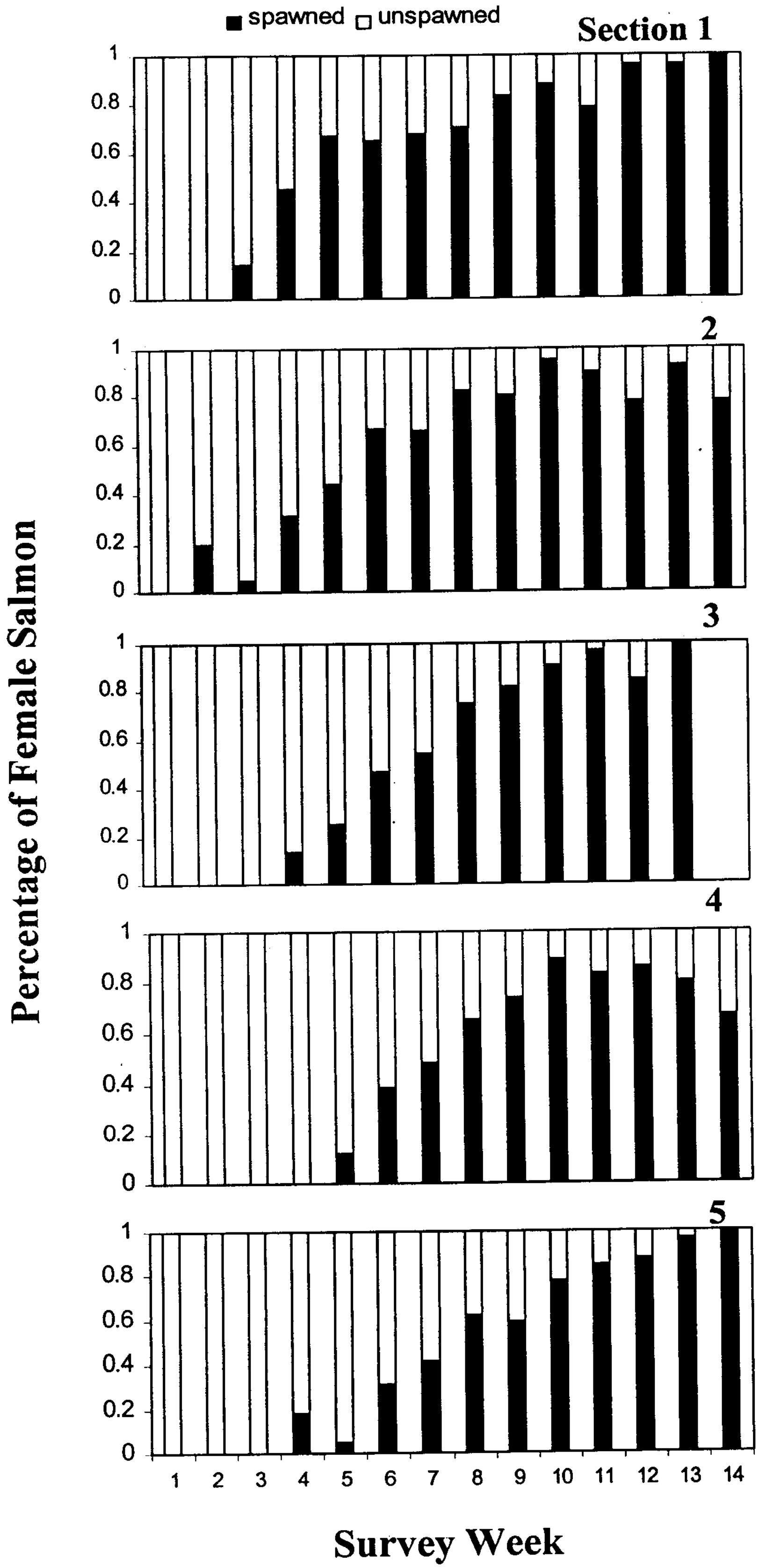

spawned
unspawned
Section 1
2
3
4
5
Percentage of Female Salmon
Survey Week
1
0.8
0.6
0.4
0.2
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14

Fig. 17

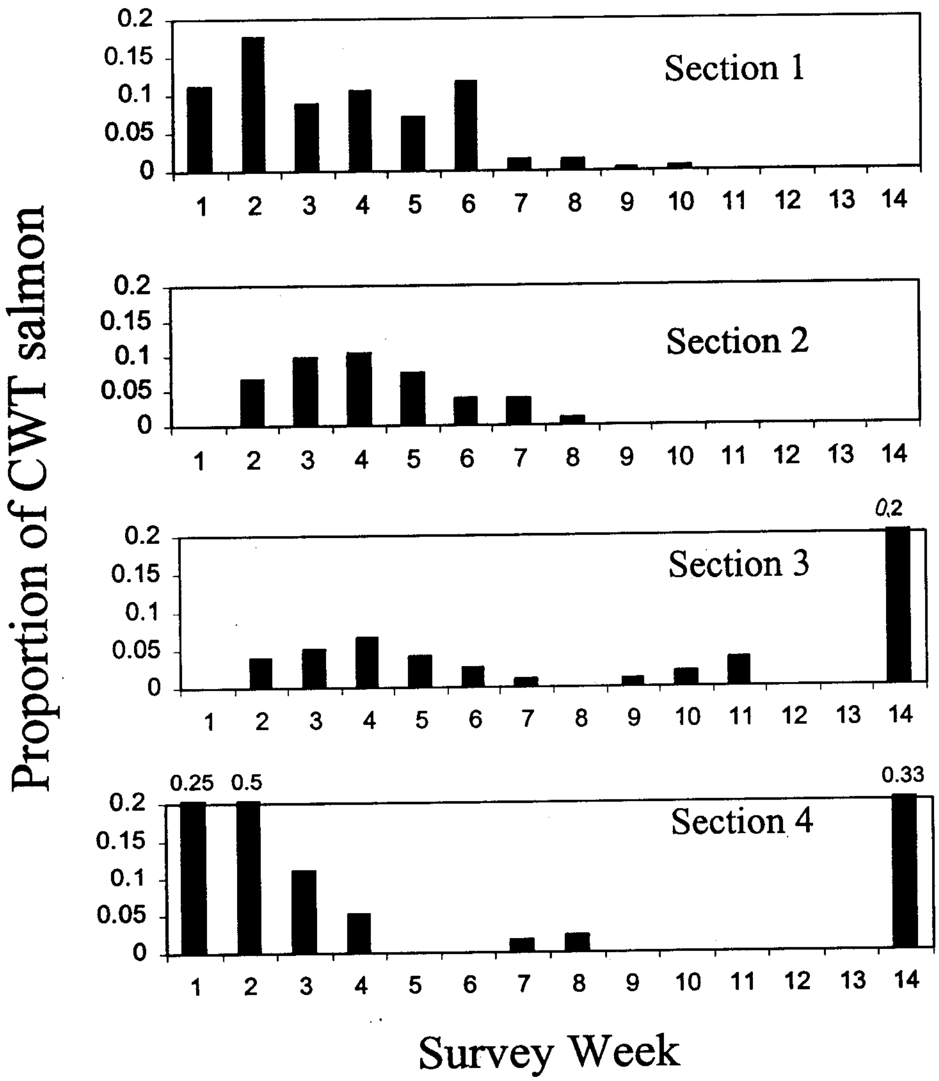

Proportion of CWT salmon
Section 1
Section 2
Section 3
Section 4
0.2
0.15
0.1
0.05
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14
0.2
0.25
0.5
0.33
Survey Week

Fig 18

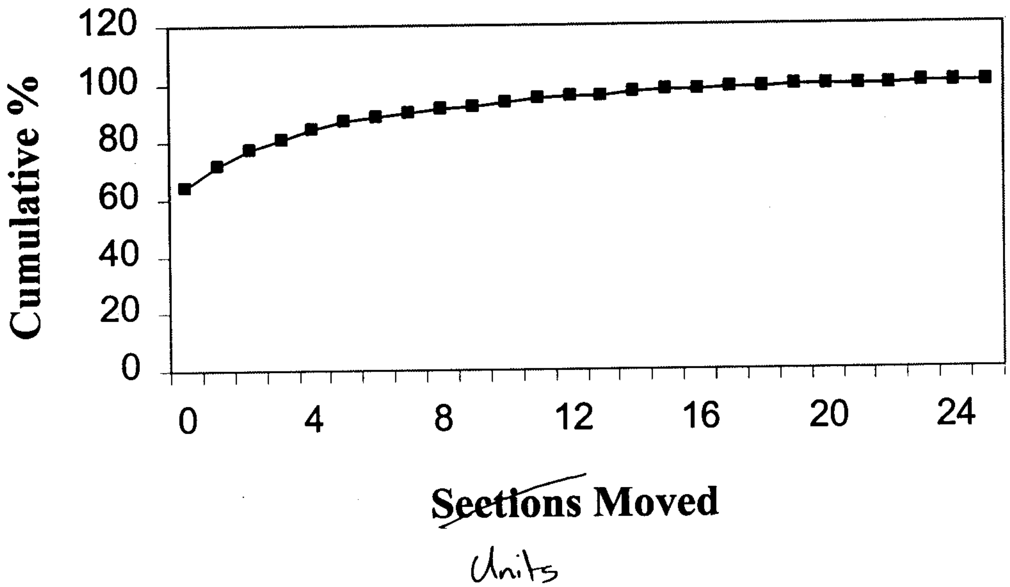

120
100
80
60
40
20
0
Cumulative %
0
4
8
12
16
20
24
~~Sections~~ Moved
Units

Fig. 19

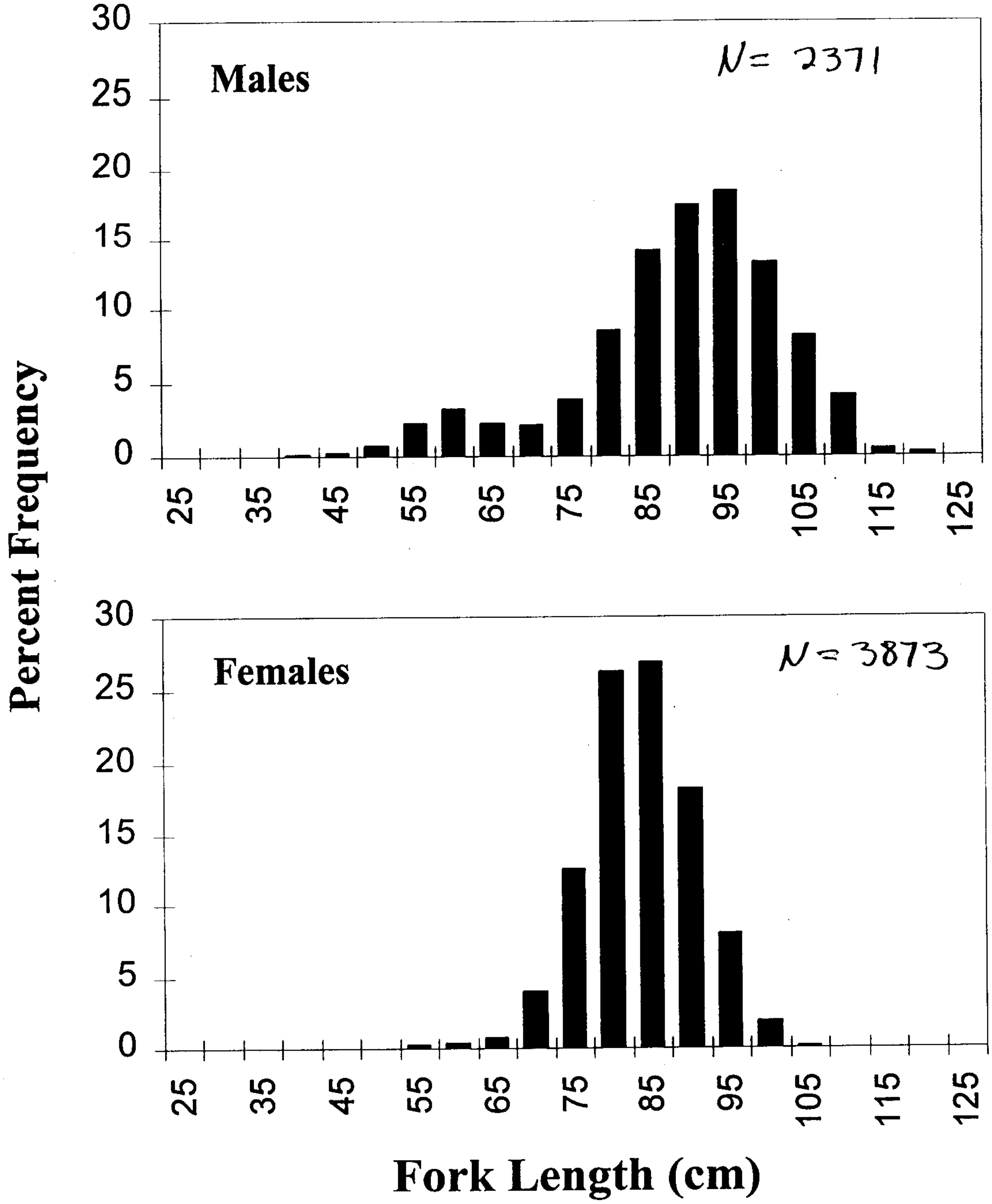

Males
N= 2371
Females
N= 3873
Percent Frequency
Fork Length (cm)
0
5
10
15
20
25
30
25
35
45
55
65
75
85
95
105
115
125

Fig. 20

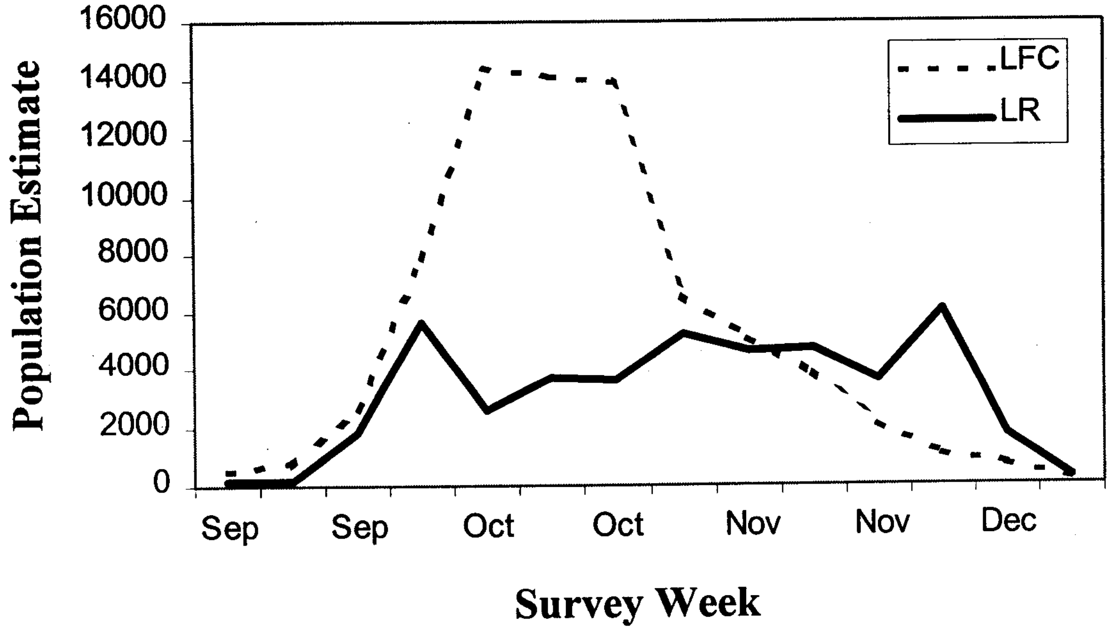

16000
14000
12000
10000
8000
6000
4000
2000
0
Population Estimate
LFC
LR
Sep
Sep
Oct
Oct
Nov
Nov
Dec
Survey Week

Fig. 21

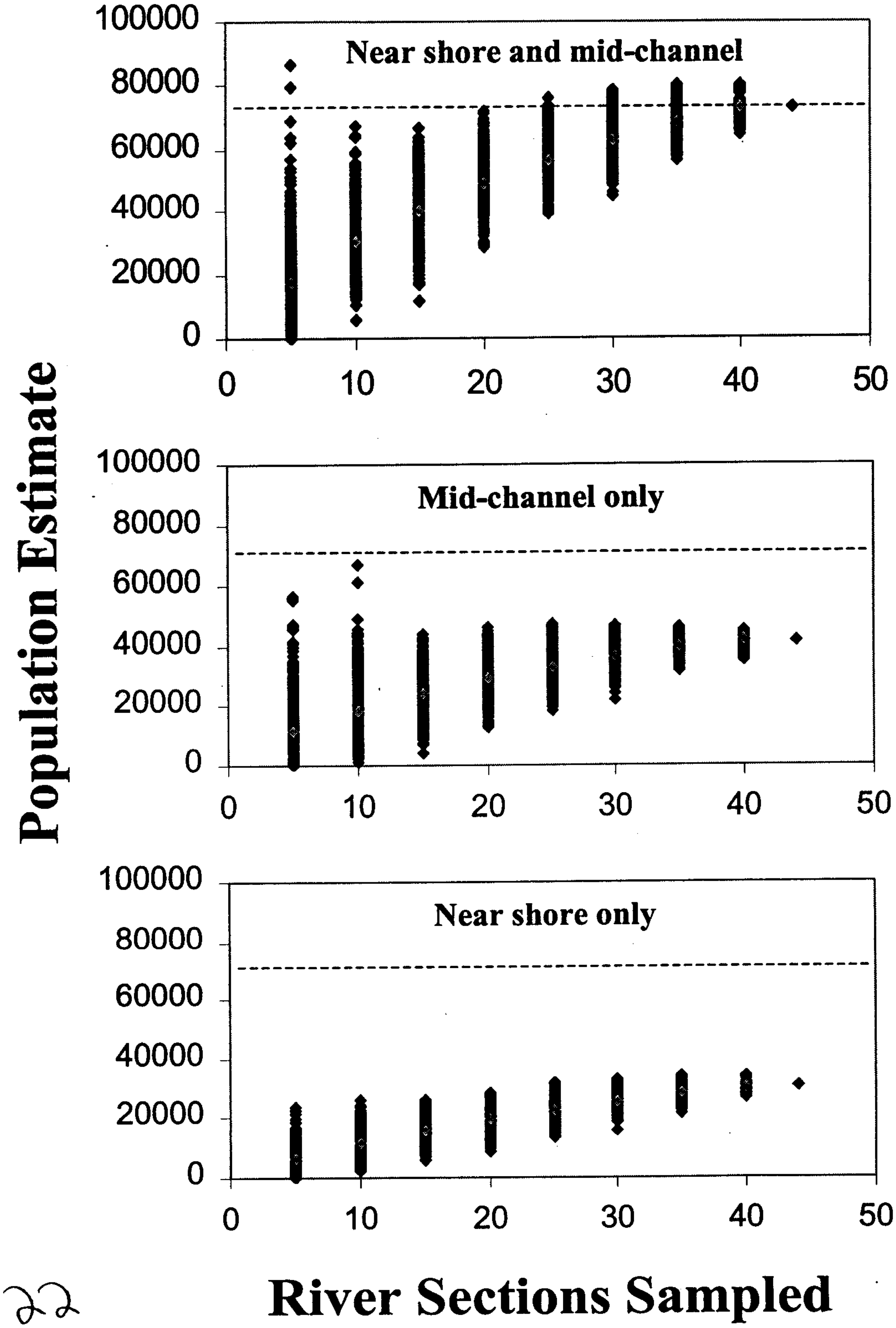
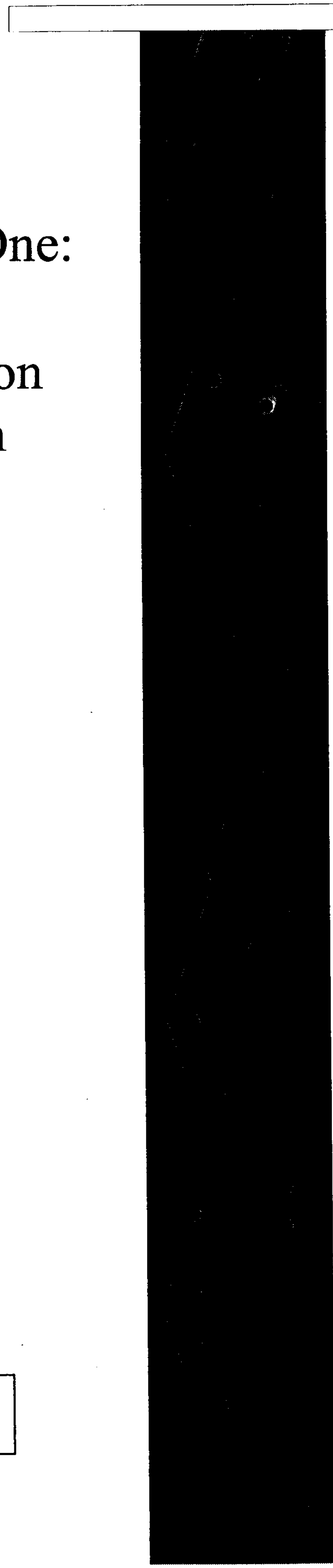

Population Estimate
Near shore and mid-channel
Mid-channel only
Near shore only
100000
80000
60000
40000
20000
0
0
10
20
30
40
50
River Sections Sampled

Fig. 22

Premise One: Random Distribution of Salmon Carcasses



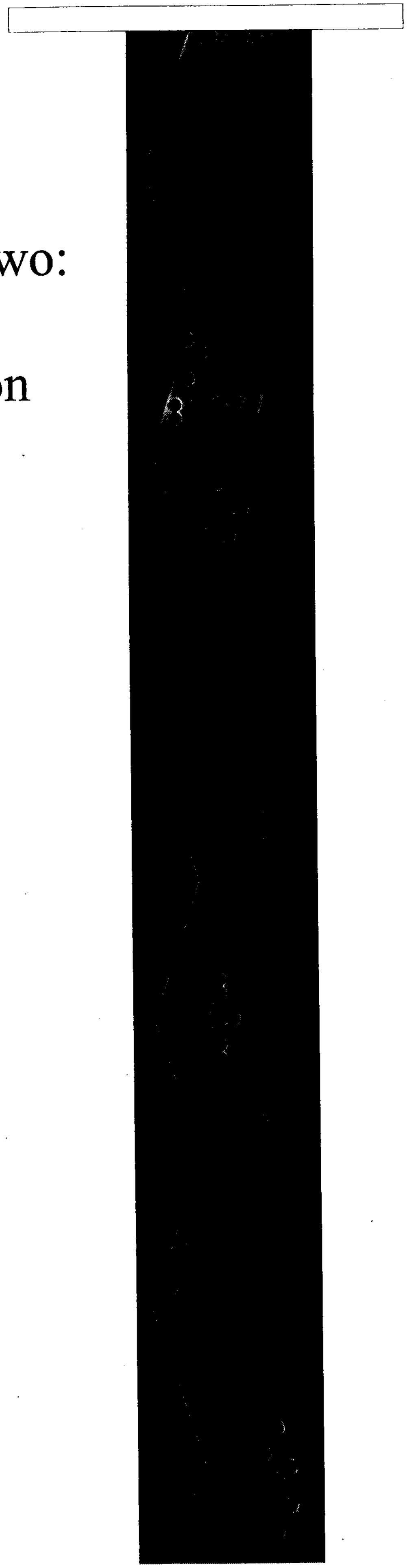
• = chopped or tagged carcass

• = carcass not captured

Figure 23

Flow

Premise Two: Patchy Distribution of Salmon Carcasses



• = chopped or tagged carcass

• = carcass not captured

Figure 24

Flow